NUTRIENT CYCLING:

I. NUTRIENT DISTRIBUTION IN SOME AMAZONIAN SOILS

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INTRODUCTION

The soils of the Amazonian forests are notoriously poor in available nutrients (Jones 1955-56). Yet these poor soils support some of the most dense, lush, natural rain forest in the world. Once these forests are cut and burned, and used for crops for one to three years, the soils will support only straggly second growth (capoeira) which will never return to the true climax forest (Duke and Black 1953). Cut-over land requires 7 to 10 years before it recovers sufficiently to support another crop.

Richards (1952) states that, "It can thus be seen that in a mature soil the capital of plant nutrients is mainly locked up in the living vegetation and the humus layer, between which a very nearly closed cycle is set up." He continues by saying, "When the forest is felled the capital of nutrients is removed or set free in the soil and the humus layer is often destroyed at the same time by burning and exposure to the sun."

Initial Observations

The author, in cooperation with F. W. Went working from the R/V Alpha Helix of the University of California, began looking at the ecology of the rain forest at Reserva Ducke 29 km east of Manaus, Brazil, and expanded these observations to the Rio Negro, Bio Branco, Rio Madeira, Taruma Acu, Solimoes, and to the Rio Huallaga and Chanchamayo Valley in Peru. Our observations showed that Richard's (1952) statements were sound. We found a concentration of feeder roots in the upper 10–15 cm of soil as have others (Corbet 1935, Jones 1955-56, Nye 1961). A closer look at these roots showed that they were growing between layers of leaves often exposed to the air and light, into dead woody fruits, and into termite galleries in dead wood. Microscopic examinations showed that the roots were laced to the dead organic matter by abundant fungal hyphae and rhizomorph tissue. Cross-sections of roots

revealed that the fungi were mostly mycorrhizal fungi (largely endotrophs) which penetrated into the cortical cells of the roots. The majority of roots examined in the "terra firme" forests which grow in areas not normally flooded, had mycorrhizal fungi while some roots observed in the "capoeira" or second growth forest, on land also free of flooding, lacked mycorrhizae. Janse (1897) found mycorrhizal root systems on 69 tree species out of 75 examined on rich Java soils. From observations, the frequency of the mycorrhizal habit appears to be at least as high in the poor Amazonian soils as in Java.

The masses of mycelium on the forest floor produced very few fruiting bodies. Fruiting bodies were most common on decaying logs which had no living plant roots penetrating them. Some logs which were very hard and suspended above ground, had few fungi and no plant roots. Other logs or stumps in contact with the soil usually were riddled by termite galleries first, with plant roots bearing fungi invading beneath the bark and into termite galleries later. Since wood has a high ratio of C to N (Corbet 1935), the presence of roots and fungi in decaying wood suggests that the internal nitrogen-fixing organisms of the termites may supply nitrogen through feces which make possible fungal decay of the wood.

The heavy, woody fruits and seeds of the Lecythidaceae contain more stored food energy than the germinating seed uses directly, but the roots of the young seedling are often seen penetrating the woody remains of the seed preceded by masses of fungal tissue. These seedlings usually have mycorrhizal roots.

The litter layer was never more than 1 to 2 cm thick except in pockets suggesting a rapid rate of decay. In Ghana in a similar climate, Nye (1961) estimated that 20,000 lbs. (9,000 kg) of organic matter is decomposed per acre per year. Coarse brownish gray sand formed the upper 45 cm with a moderately hard yellow clay below. For a discussion of the plants from these sites, see NUTRIENT CYCLING II NUTRIENT DISTRIBUTION IN AMAZONIAN VEGETATION (Stark).

Moribund termite mounds on the soil surface were often completely penetrated by living roots and fungi. In general, soil animals were scarce in these sands compared to lateritic soils in Surinam and Puerto Rico. The Brazil sands had a few species of ants and termites, but no earthworms. Ants and termites may be very important to decay in the tropics since they are abundant.

In light of our initial observations and data and those of many others, a hypothesis was developed which stimulated this research on nutrient distribution. The "direct nutrient cycling hypothesis" explains the manner in which plants with mycorrhizal roots conserve and utilize nutrients. It is called "direct" because the soluble phase of nutrients in the soil is bypassed, since most nutrients are passed from dead organic matter by mycorrhizal fungi to living roots (Went and Stark 1968 a & b). This hypothesis poses a closing link in Richards (1952) "nearly closed cycle." Previously, it was thought

that the surface network of roots alone was sufficient to catch most of the nutrients released from litter, but the absorbing area of the feeder roots alone is relatively small for massive uptake. Climax forest roots had few root hairs. This paper examines the nutrient distribution in soils, while a second paper describes the nutrient distribution in plants to see where the bulk of readily available nutrients occurred. Recent studies show that radio nuclides are readily transferred from dead litter to living roots (organic to organic) without entering the soil.

Hypothesis

The "direct nutrient cycling hypothesis" states that:

I. The nutrients in the Amazonian rain forest ecosystems are held largely in the organic phase, in living roots, wood, bark, and leaves, and in dead organic litter. These are few nutrients available in the heavily leached soils which have high percentages of SiO_2 (Sioli 1966) (Fig. 1). Nutrients are added to the system from rain water and weathering zones tapped by deep roots (Greenland and Kowal 1960).

II. The majority of plants in the climax rain forest have mycorrhizal root systems (Janse 1897) and appear to be capable of using concentrations of nutrients in dead wood and litter. Some plants in the "capoeira" do not have surface mycorrhizal root systems and are adapted to concentrate nutrients from a diffuse supply in the soil.

III. Plants in the climax forest accumulate nutrients in living parts which are shed to the ground forming litter (Corbet 1935). Some trees appear to be able to withdraw nutrients from old leaves before they are shed. Leaching of living leaves, litter fall suspended in the canopy, epiphytes, feces, and stem flow during rains releases soluble nutrients into the soil.

IV. The fungal partners in mycorrhiza, together with help from bacteria, animals, and other members of the rhizosphere are capable of breaking down dead organic litter and can pass nutrients in some form to the living tree root cells. Only a small amount of nutrient is thought to leak into the soil past the root and fungal mat from rain, bacterial decay, and feces, with the bulk being transferred directly from dead litter to living roots via hyphae (mainly endotrophs). Some mycorrhizal fungi may fix nitrogen (Becking 1965). Soil animals, except for ant and termites, are probably less important here than in richer soils.

This mycorrhizal habit of nutrition is well known for orchids, but has not been proposed for tropical rain forest trees. In the temperate forests, mycorrhizal fungi are known to pick up soluble P and N and possibly other nutrients from the soil and pass these to the living roots (Henry 1966).

V. Wood appears to be invaded first by termites with internal N_2-fixing organisms (Corbet 1935). The feces of the termites may contain enough nitrogen to allow the mycorrhizal fungi to decompose the wood and pass materials to the living roots. The feeder roots appear to grow with their mycorrhizal associates to the substrate, *i.e.* dead organic litter. Thus, the feeder roots

often exhibit negative geotropism in a manner that suggests that they may have a chemotropnic response to organic matter.

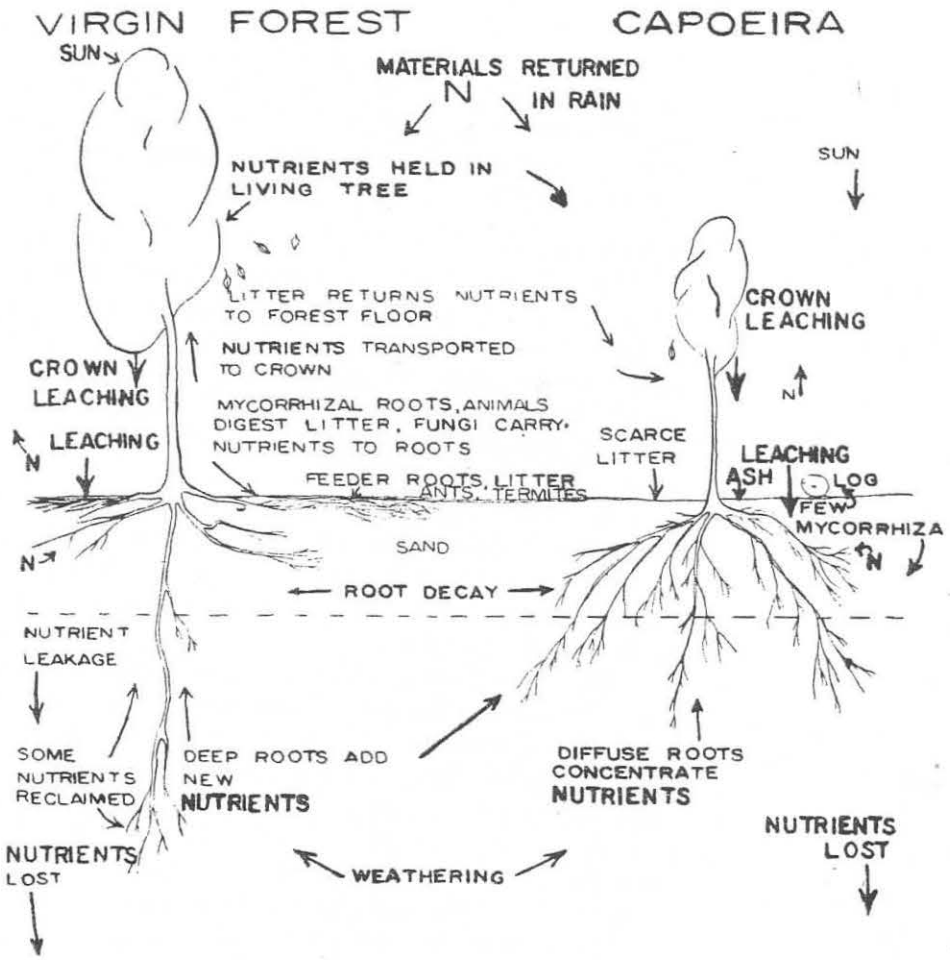

Fig. 1. Simplified diagram of direct nutrient cycling in the climax or virgin forest and nutrient cycling in the "capoeira" of the Amazon Basin. "N" refers to the movement of nitrogen in its various forms.

VI. Some trees, especially those in the Lecythidaceae, may concentrate nutrients in their heavy woody fruits and seeds. These nutrients are thought to be freed by cellulose-digesting mycorrhizal fungi (Farrow 1954) in the roots of the seedling after germination and could aid in the early growth of the seedling. Seedlings on the forest floor do survive years of low light intensities, possibly because they may receive food through mycorrhizal fungi to augment food produced by photosynthesis. The fungi may also take growth substance from the roots.

VII. The plants of the "capoeira" appear to have few surface mycorrhizae. They also have extensive, deep, diffuse, net root systems suggesting that the plants may be able to concentrate nutrients which were made soluble after cutting and burning and were dispersed throughout the soil. The initial rapid growth of "capoeira" suggests that these "secondary pioneers" are capable of rapidly tying up nutrients which are soluble and will be readily leached or carried away in run-off water. Mycorrhizae adapted to nutrient uptake from soil may be important in some second growth vegetation (indirect nutrient cycling).

VIII. After the "capoeira" vegetation completes its relatively short life span, some members of the original climax forest with mycorrhizal roots return and begin to use the nutrients stored in the dead litter from the "capoeira" (Fig. 1). If a prolonged dry period occurs, savanna develops instead of rain forest (Hardy 1945).

IX. The draining of the Miocene lakes about 25 million years ago during the uplift of the Andes left behind alluvium poor in nutrient bearing minerals (Hardy 1945, Klinge 1965, Marel 1947). Leaching from heavy rains may have depleted the soil nutrients faster than additions from the atmosphere and weathering could deliver new nutrients. During this period, plants with diffuse roots may have become dominant by storing nutrients from the soil in their organic matter (indirect nutrient cycling). As the soil became poorer, mycorrizal plants may have assumed dominance because they were not completely dependent on the soil for nutrients. A large, lush, climax forest evolved which was closely adapted to economical nutrient utilization and to nutrient conservation.

X. Leaching has continued to remove part of the nutrients added from the air and weathering, and from non-mycorrhizal decay while the plants have captured a portion of these nutrients. As the total of biologically important nutrients is slowly depleted through leaching and the root zone loses more of the weatherable minerals, there may come a time when no new nutrients can be released from the level sands and additions from rainfall will not be sufficient to support tall forest. Leakage of nutrients from the organic system over thousands of years could produce conditions unfavurable to large plants. Cutting and burning accelerates this decline in nutrients (Nye and Greenland 1960). Renewal of the system would require uplift and erosion of the weathered minerals, or deposition of nutrient bearing sediments with a zone accessible to roots. Direct nutrient cycling has probably evolved in other areas to different degrees.

METHODS

Sampling Sites

Twelve sampling sites were used in five main areas (Fig. 2). Of the 3 main sites at Reserva Ducke (A, B, C,) subsites were selected using random

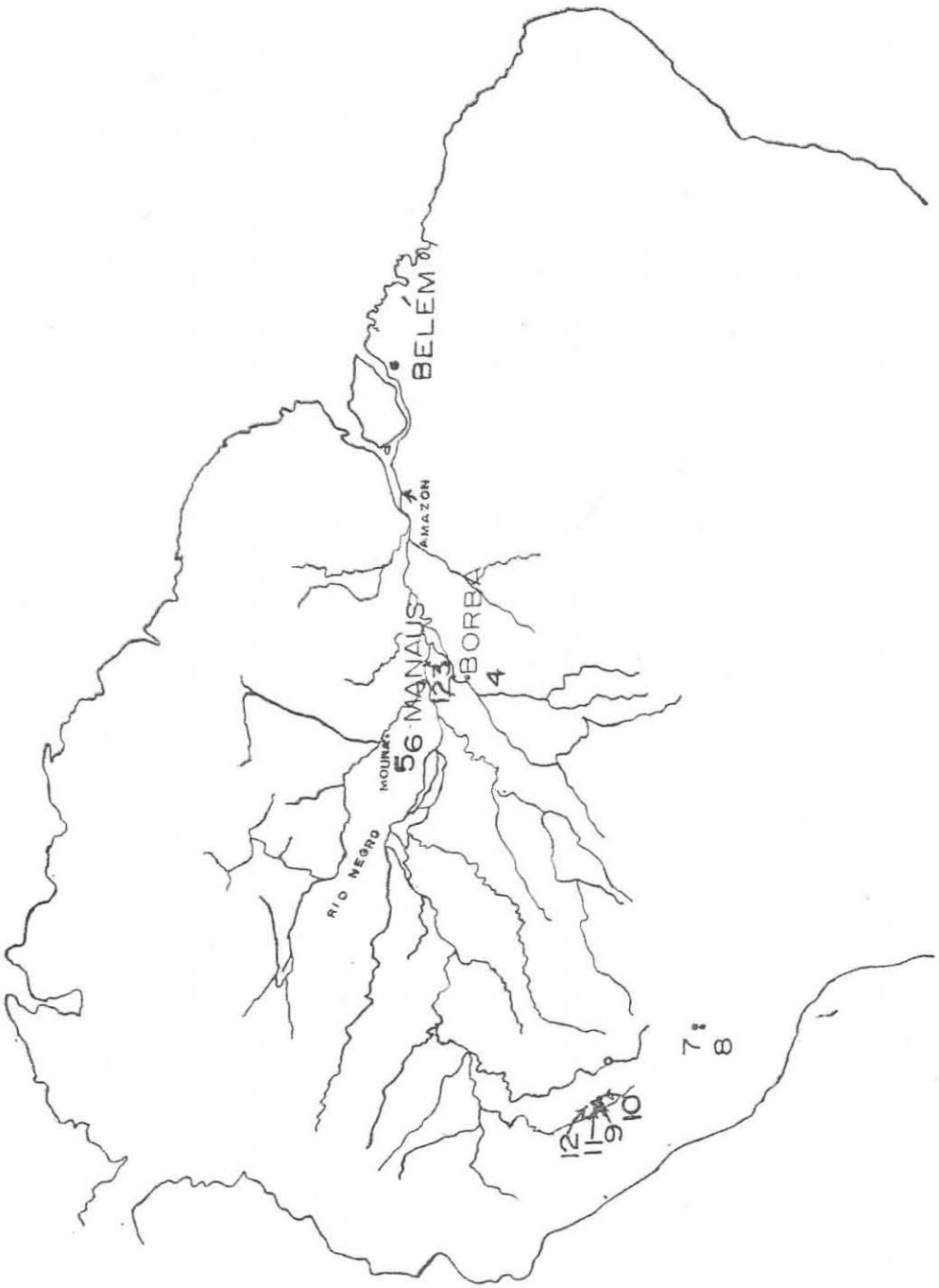

Fig. 2. Map of northern South American showing twelve main sampling sites. 1=Ducke A. 2=Ducke B. 3=Ducke C, 4=Borba, 5=Rio Negro-Branco, 6="Capoeira", 7, 8=Chanchamayo Valley, Peru, 9–12=four sites near the Forestry Camp of the Universidad Agraria, Peru.

numbers keyed to a map of the forest trees and sections, so that 10 sampling sites fell in the non-flooding *"terra firme"* and 5 fell in the flooding zone (random within vegetation types).

1. Reserva Ducke (referred to as "Ducke") is 29 km east of Manaus (Fig. 2, sites 1, 2, 3). The elevation is about 50 m with range in average annual relative humidity from 73 to 82%. All sites occurred in heavy rainfall areas with one to three months of dry season. June air temperatures average 25°C while September air temperatures average 30°C (Hewitt 1966, Marbut and Manifold 1926).

Sites A and B of Reserva Ducke were on *"terra firme"* and consisted of spodosols. A thin litter layer (1–2 cm) occurred above the grayish brown sand which had a 1 to 2 cm organic humus zone. At 45 cm, the sand graded into a hard sand with some clay. No iron or calcium concentrations were found, although these may occur deeper than 60 cm. The zones of illuviation and elluviation were poorly defined.

The vegetation consisted of many trees to 30 m high, mainly Leguminosae, Lecythidaceae, and Sapotaceae. *Eperua bijuga, Lecythis paraensis, Couepia elata, Vantanea* sp., *Brosimum* sp., *Lucuma* sp., *Virola* sp., and *Sclerolobium* sp., were common in this forest type (Takeuchi 1961). Site A had larger, more lush vegetation than did Site B.

Site C in Reserva Ducke was "igapo" or fluvial forest adjacent to a stream that floods each year. Sampling included the wettest and the driest locations. The soil was a heavy black humic sand with masses of roots down to the mottled, hard sandy clay layer. Palms (*Mauritia* sp.) were dominant on this site with some trees (*Eschweilera* sp.).

2. The site on the Rio Madeira was 36 km southeast of Borba (Fig. 2, site 4). The sampling was from *"terra firme"* with similar soil but more lush vegetation than at Reserva Ducke. Mineralogical analyses showed 61.5% SiO_2 and 15.2% Al_2O_3 (Table 1). Mechanical analyses showed 87.0% sand and 9.8% silt and clay at 20–22 cm. This soil appeared to be podzolized.

3. The main site on the Rio Negro (referred to as "Rio Negro-Branco) was about 11 km west of Moura (Fig. 2, site 5). This was low *"terra firme"* according to the terminology of Takeuchi (1961). The area surrounded by lower land does not flood, but the water table may be high at times. The surface soil had up to 15 cm of dark humus laced with fungal mycelia and partly decomposed leaves overlying a grayish sand grading to a sandy clay spodosol). Mineralogical analyses showed 94.0% SiO_2 and 4.4% Al_2O_3 with no concretions in the sand at 20–22 cm (Table 1). Palms such as *Mauritia flexuosa, Euterpe oleracea, Oenocarpus* sp., and *Iriartea* sp., grew with *Brosimum* sp., *Symplomia* sp., *Eschweilera* sp., *Vismia* sp., and *Carapa quianensis* in this forest type (Takeuchi 1961).

4. The second site on the Rio Negro was "capoeira" or second growth on similar soil adjacent to the river and rarely flooding (except for sample 3, Fig. 2, site 6). The climax forest now 3 km away once grew here, but cutting and burning four years before had brought in *Cecropia* sp., *Triplaris surinamensis*

both myrmecophiles), Melastomaceae (shrubs), and *Heliconia* sp. No humus layer occurred and the sands were a medium to light brown grading into light brown sand at 20–22 cm.

5. The six sampling sites in Peru (Fig. 2, sites 7–12) were at San Ramon-La Merced and La Francia in the Chanchamayo Valley, and at the Forestry Camp of the Universidad Agraria (Aucayaco) along the Rio Huallaga. The vegetation and soils for the lowland and midland sites were similar with more palms in the lowland forest. *Hura crepitans, Lucuma* sp., *Lecythis paraensis,* and *Iriartea* sp. grew there. The soils were obviously richer with lusher growth than occurred at Reserva Ducke or other sites in Brazil, and more feeder roots penetrated to 60 cm than elsewhere. Peruvian data were lumped in order to compare these results to those from Brazil. Mineralogical analyses classed these soils as nonlateritic sands and sandy clays with 64.0% SiO_2 and 14.8% Al_2O_3 at 20–22 cm depth. The Copal highlands and the San Ramon-La Merced sites were derived from limestone with a 0.4 to 1.5 m soil depth over solid rock supporting varied, low forest.

Analyses of Soils

Twelve main study sites were used in Brazil and Peru. The three plots (A, B. C) at Reserva Ducke were randomly located (Within soil types) as were the subplots. Five plots each were sampled from Borba, Rio Negro-Branco, "Capoeira" (second growth), and two each from 6 locations in Peru.

TABLE 1. *Mineralogical[1] and mechanical analyses of Brazil and Peru soils (litter and humus layers not included)*

Location	Depth cm	Minerals (%)				Mechanical Analyses(%)		
		SiO_2	Al_2O_3	SiO_2/Al_2O_3	2 Class	Sand	Silt & Clay	Other (Gravels)
Peru								
Aucayaco Lowland	0-4	70.9	9.4	7.5	NL	79.0	19.9	1.1
Aucayaco Lowland	20-22	64.0	14.8	4.3	NL	67.0	32.7	0.3
Brazil								
Reserva Ducke (A-C)	0-4	—	—	—	—	95.2	1.2	3.6
Reserva Ducke (A-C)	20-22	76.8	13.6	5.6	NL	58.2	36.9	4.9
Reserva Ducke (A-C)	60-62	72.6	15.3	4.7	NL	74.4	16.1	9.5
Borba	0-4	—	—	—	—	97.2	1.9	0.9
Borba	20-22	61.5	15.2	4.0	NL	87.0	9.8	3.2
Rio Negro-Branco	0-4	—	—	—	—	78.0	17.8	4.2
Rio Negro-Branco	20-22	94.0	4.4	21.3	NL	56.2	43.7	0.1
"Capoeira"	0-4	—	—	—	—	95.8	2.7	1.5
"Capoeira"	20-22	—	—	—	—	89.1	10.5	0.4

1 X-ray fluorescence. Surface samples contained too much organic matter for analysis by this method.

2 "NL" refers to probable podzolized soils which are definitely non-laterctic according to the classification of Martin & Doyne (1927).

The upper 4 cm with soil and roots was severed around a 10×10 cm template using a sharp knife. Roots between 0.05 and 1 mm diameter were separated from the soil. The remaining soil was air-dried and stored. Composite soil samples from areas 1×1 m were taken from 10 random locations in each vegetation type at Reserva Ducke from 0–4 cm, 20–22 cm, and from 60–62 cm.

Soil pH on air-dried samples was measured with a pH meter using 2.5 : 1 soil : water ratio.

The approximate percent organic matter was measured by ashing a 1 g sample at 525° (± 3) C for 2 hours and weighing the residue. This method gives only the approximate percent organic matter (plus ash) since some volatiles, bound water, N and P are probably lost during ignition (over-dried samples 65° ± 1°C for 24 hours).

The soil was mixed thoroughly and subsamples were ground and homogenized. Duplicate gram samples of soil dried at 65°C (± 1C) were digested twice in Teflon beakers in a sand bath using concentrated $HCLO_4$ and HF. The nearly dry material was taken up in 6N HCL and made to 100 ml. The standards were made with 6N HCL. Highly organic soils were predigested with HNO_2 and the tri-acid mixture used with plant material. The total elemental content of soils was measured to determine what levels of reserve nutrients remain in the soil to be released by weathering.

Those elements most needed by plants were measured, and "total" refers to ten elements of biological importance. The elements, Cu, Fe, Zn, Ca, and Mg were measured using standard methods for a Perkin-Elmer atomic absorption spectrophotometer (Allan 1958, 1959, 1960, 1961; Clark 1960; David 1958, 1959; Hewitt 1966). One percent lanthanum was used in samples and standards where Ca and Mg were to be measured. The elements Na and K were measured from the $HCLO_4$–HF digestion process using a Beckman flame photometer, and P was measured colorimetrically by the vanadomolybdophosphoric yellow color. Total nitrogen was determined by the modified Kjeldahl method (separate digestion). All results were expressed as microgram per gram of dry matter. Duplicate determinations of elements in homogenized soil samples were made and analyzed for percent variability (under 5%). Since most soils devoid of organic matter did not produce a measurable level of total phosphorus with standard methods, the soil samples were analyzed for percent organic phosphorus. Ten percent acetic acid and 30% H_2O_2 (Marel 1947) were used to determine what percentage of P occurred in the organic phase.

Determinations of the cation exchange capacity of the soil required three washings each of 1 N NH_40Ac (pH 5.2) as an extractant, 1 N $CaCl_2$ for saturation, 30% acetone as a flushing solution, and 1N NH_40Ac (pH 7.0) as final extractant. The 1 N NH 0Ac used as the initial extractant was saved and the levels of NH_40Ac extractable Ca and Mg were measured by atomic absorption spectrophotometry, and the Na and K were measured by flame photometry. Cation exchange capacity was measured as ppm Ca (converted to meq|100 g) in the final extractant using atomic absorption spectrophotometry.

Mechanical analyses were made on twelve oven–dry soil samples from Brazil and Peru using soil sieves. Mineralogical analyses from 20–22 cm and 60–62 cm of six representative soil areas were made using X–ray fluorescence. These data with soil color and texture were used to classify the general type of soil.

An analysis of variance was made on the elemental determinations of soils and plant materials, and significant differences noted as "–", significant at the 5% level, and "––", significant at the 1% level.

RESULTS AND DISCUSSION

Analyses of Soils

Mineralogical analyses showed that the Amazon soils were spodosols with from 61.5 to 94.0% SiO_2 and from 4.4 to 15.3% Al_2O_3 in the upper 20 cm (Table 1). The SiO_2/Al_2O_3 ratios from 20 cm varied from 4.0 to 21.3 classfying them as nonlateritic in the upper 60 cm. The Brazil soils had slightly less SiO_2 and slightly more Al_2O_3 than was reported by Marbut & Manifold (1926). Observations suggest that some laterite may occur at levels below 60 cm.

Mechanical analyses (Table 1) indicated that the soils studied have from 58.2 to 97.2% sand with smaller fractions (1.2–36.9%) silt and clay. The surface sand had a small amount of organic matter (humus) coloring the upper 0–2 cm, except on the wettest sites which were brown or black to 30 cm. The "capoeira" or second growth forest soil had 0–1 cm of humus.

a. Organic Content

There was a strong decrease in the organic content of the soils from 26.2% at 0–4 cm to 6.1% organic at 60–62 cm in Peru. At Ducke A, a dry "*terra firme*" forest, the surface 0–4cm had 14.8% organic matter, while only 4.0% occurred at 60–62 cm (Table 2). The 0–4 cm organic content is considerably

TABLE 2. *Average percent organic content of three depths on Amazon soils*

	%Organic matter with depth—cm		
Location	0-4	20-22	60-62
Peru	26.2	10.6	6.1
Brazil			
Ducke A	14.8	7.2	4.0
Ducke B	17.3	4.2	—
Ducke C Wet site	28.7	—	3.7
Borba	40.9	—	—
Rio Negro-Branco	24.0	15.3	—

higher than the 6.5% reported for New Guinea spodosols (Mohr and van Baren 1954). This decrease in organic content with depth was reported by Cunningham (1962) for Ghana soils and by Mohr & van Baren (1954) for New Guinea. Tables 3 and 4 show that the pH and cation exchange capacity also decreased with depth. Peru, Ducke C, and Borba soils tended to have the highest organic contents in the 0–4 cm level (26.2, 28.7 and 40.9 % respectively).

b. Acidity

The soil surface (0–4 cm) pH was highest in Peru (6.1), and lowest at Borba (3.7, Table 3). The Brazil soils ranged in pH from 4.0–4.4 at 0–4 cm, to pH 4.0–4 at 60–62 cm depth. In Peru the trend was toward alower pH with greater depth (6.1–5.3, Doyne 1935). At Ducke A, B, and C, the pH

TABLE 3. *Average pH with soil depth from the Amazon.*

Location	pH with depth (cm) 0-4	20-22	60-62
Peru	6.1	5.9	8.3
Brazil			
Ducke A	4.4	4.0	4.2
Ducke B	4.1	4.2	4.4
Ducke C Wet site	4.0	4.2	4.6
Borba	3.7	3.6	—
Rio Negro Branco	4.2	4.2	4.1
"Capoeira"	4.3	4.1	4.0

tended to become higher with depth (4.0–4.6). Other Brazil soils studied decreased in pH with depth (4.2–4.1 or 4.3–4.0 for the "capoeira"). Higher pH with depth could indicate zones of cation accumulation.

The high acidity of these soils explains why low levels of extractable cations were found in the soils with the highest cation exchange capacity (Table 4). Some of the cation bonding sites must hold hydrogen ions to produce strongly acid soils.

c. Cation Exchange Capacity

The average cation exchange capacity (C.E.C.) of all depths of Peru soils studied ranged from 3,900μg/g at 60 to 62 cm, to 6,388μg/g at 0–4 cm and was significantly higher th[illegible] Brazil soils which were studied (except for the high C.[illegible] [illegible]–22 cm from the wet site, Ducke C, Table 4). Ducke B had 5,268μg/g C.E.C. in the surface horizon which was high in organic content. Ducke A surface soil had a low organic content and

C.E.C. (1,880μg/g), with 1,785μg/g at 60–62 cm (Table 4). Although C. E.C due to organic matter was not determined, I believe much of the exchange capacity resides in the organic fraction of the soil. Rio Negro-Branco and most other soils tended to decrease in C.E.C. with depth. Since organic matter also decreased with depth while percent clay increased (Table 1, 2), C.E.C. appears to be most closely related to organic content. The Rio Negro-Branco "capoeira" increased in C.E.C. from 1,403μg/g at 0–4 cm to 1,839μg/g at 20–22 cm (limited data). Since this area has been burned and heavily leached, there may have been a downward movement of colloids. The low C.E.C. agrees with the results of Cunningham (1963) on burned Ghana forest soils. The C.E.C. of the deeper Amazon soils in general (except for Peru) is much lower than that reported for acid Ghana soils (Cunningham 1963, Moore and Adetunji 1966) and is nearer to those from Surinam (Schulz 1960). Few agricultural soils are known to have a C.E.C. as low as 7.0 meq|100g soil (Table 4).

TABLE 4. *Average cation exchange capacity, percent saturation of exchange capacity, total soil cations, average sum of ammonium acetate extractable cations and percent of total cations left in nonextractable form for Amazonian soils.*

Location	Depth: cm	Av. C.E.C. μg/g	Av. C.E.C. meq/100g	% Saturation	Total Soil cations μg/g	Av. Sum of Extractable cations μg/g	% Total cations-nonextractable
Peru	0-4	6,388	31.9	21.6	30,465	1,356	94.6
	20-22	4,240	21.2	10.8	22,922	576	96.4
	60-62	3,900	19.5	13.7	32,238	503	97.5
Brazil							
Ducke A	(0-4)	1,880	9.4	6.2	1,280	70	94.8
	20-22	1,360	6.8	9.3	1,609	57	98.5
	60-62	1,785	8.9	3.8	1,642	25	98.6
Ducke B	0-4	5,268*	26.3	4.9	1,526	180	93.4
	20-22	1,511	7.6	3.1	1,579	113	92.5
Ducke C	0-4	4,412*	22.1	9.8	1,781	211	87.9
	20-22	4,725*	23.6	2.7	1,824	135	92.9
	60-62	750	3.7	3.0	1,797	28	96.6
Rio Negro-Branco	0-4	2672	13.4	19.5	2,504	526	79.0
	20-22	2,019*	10.1	28.5	2,140	774	63.4
"Capoeira"	0-4	1,403	7.0	11.9	1,901	95	94.9
	20-22	1,839	9.2	19.8	2,198	244	89.1

*High organic content.

The Peru soils showed a moderately high percent saturation of available bonding sites (average of 21.6% at 0–4 cm and 13.7% at 60–62 cm, Table 4). The Ducke soils tended to decrease in percent saturation with depth with a 20–22 cm zone of higher saturation at Ducke A (Table 4). The Rio Negro-

Branco soils both increased in percent saturation from 0–4 cm to 20–22 cm. At both levels, the "capoeira" had a significantly lower percent saturation than did the climax Rio Negro-Branco forest. The surface levels of Rio Negro-Branco were high in organic content and had deep humus layers not included in Table 2 which may explain the relatively high saturation. The 11.9 and 19.8% saturation of available bonding sites in the "capoeira" soils is significantly higher than the saturation levels of the Ducke soils and lower than that of the Rio Negro-Branco soils suggesting that there were adequate bonding sites in the "capoeira" soil capable of retaining some of the elements which were freed after burning about four years ago. The percent saturation of all soils studied was much lower than the 50% found in Ghana soils.

d. Extractable Soil Cations

The average sum of ammonium acetate extractable cations is used to indicate the levels of Na, K, Ca, and Mg which should be readily available to plant roots (Table 5). Obviously this is a rough approximation since we do not know the true nature of the chemical extractant given off by plant roots The Peruvian soils had the highest μg/g of extractable cations (503–1,356μg/g, Table 4) with the Rio Negro-Branco area almost as high (526–774μg/g). The Rio Negro-Branco "capoeira" soil was extremely low in extractable cations (95–244μg/g) and was much lower than the adjacent climax forest soils, but slightly higher than the Ducke areas (Table 4). The sum of extractable cations was very low compared to that of most temperate agricultural soils, or to New Guinea podzols (2,000–4,600μg/g (Mohr and van Baren 1954)).

The pattern of extractable cations followed that of the C.E.C., i.e. decreased with depth except for the Rio Negro-Branco, Ducke C, and "capocira" areas (Table 5). A comparison of the extractable cations and C.E.C. shows that these soils are capable of bonding many more cations than they presently hold suggesting that heavy leaching has depleted the biologically important cations. Additions of fertilizer might temporarily restore the soils' fertility, but leaching would make fertilizer application expensive.

The μg/g of ammonium acetate-extractable Na, K, Ca, and Mg are highest for Peru soils as would be expected (Table 5), with Rio Negro-Branco so.ls as high or higher in Na and K. The ranges of extractable cations which are given are quite broad because 5 to 10 sampling sites are combined in the range figures. For good agricultural soils, 65% of the exchange complex should be occupied by Ca, 10% by Mg, 5% by K, and 20% by H (American Society for Agronomy 1949). Clearly, such a relationship does not exist in the Amazon soils (Table 5). These soils are poorer in extractable Ca, Mg, Na. and K than were the Guatemala soils (Snedaker and Gamble 1969). Levels of 10 to 29μg/g extractable Ca or 1 to 36μg/g of Mg will not support the poores sugar cane. This explains the burning practice which is so common in tropical agriculture. Unless the existing vegetation is burned, there are no enough nutrients in the soils of many areas to support even those crops with low nutrient demands.

There is no clear-cut pattern of elemental distribution by depth. The Rio Negro-Branco climax forest had fairly high levels of Na (av. 50–131 μg/g), but low levels of Ca (av. 7–11 μg/g and Mg (av. 6–36 μg/g), while the neighboring "capoeira" had much lower levels of all elements except Ca (av. 29–31 μg/g). This provides further evidence of leaching of the exposed "capoeira" soils and suggests that small amounts of Ca were bonded against loss. Only the Peru soils had sufficient levels of K, Ca, and Mg to support reasonable growth independent of direct nutrient cycling and nutrient conservation.

TABLE 5. *Average and ranges of ammonium acetate extractable cations from three depths of Amazon soils (based on 5 to 10 samples and as micrograms per gram of soil).*

Location	Depth cm		Na		K		Ca		Mg	
			μg/g							
Peru	Range	0-4	10-25		250-460		600-1070		48-180	
	Av.			16		342		892		80
	Range	20-22	13-22		103-182		50-425		23-43	
	Av.			18		132		267		34
	Range	60-62	15-40		13-226		75-295		24-175	
	Av.			22		109		239		77
Brazil										
Ducke A	Range	0-4	15-30		12-60		5-18		2-5	3
	Av.			20		29		11		
	Range	20-22	—		12-14		4-6		2-4	
	Av.			—		12		5		3
	Range	60-62	3-5		12-15		5-10		2-7	
	Av.			4		12		6		4
Ducke B	Range	0-4	4-20		28-118		5-40		1-18	
	Av.			11		67		12		10
	Range	20-22	5-25		14-195		3-108		2-28	
	Av.			12		64		26		11
Ducke C	Range	0-4	4-13		24-320		5-30		17-39	
	Av.			5		139		19		25
	Range	20-22	4-21		12-67		10-100		3-7	
	Av.			15		36		67		5
	Range	60-62	4-16		9-18		6-12		1-1	
	Av.			14		14		10		1
Rio Negro-Branco	Range	0-4	11-100		380-650		6-30		8-76	
	Av.			50		410		11		36
	Range	20-22	120-140		378-780		4-16		2-10	
	Av.			131		629		7		6
"Capoeira"	Range	0-4	12-24		30-74		10-65		3-8	
	Av.			16		45		29		4
	Range	20-22	9-14		14-34		20-38		5-8	
	Av.			10		24		31		6

The extractable cations of the sands of the Brazil spodosols might be compared quantitatively to the composition of nutrient solutions used in sand cultures of crop plants. The bleached sands devoid of surface litter are, in

many respects little different from sand culture media. The cations extractable from the sand should represent, roughly, what is available to the plants. The cations in the balanced nutrient solution used on sand are all available to plants.

Nutrient solutions as described by Hewitt (1966) are usually supplied with adequate to a slight excess of balanced cations to encourage rapid growth. For this reason, it may not be completely fair to compare the levels of extractable soil cations to the cation levels in nutrient solution. The latter are usually applied daily or at least weekly. Since a gram of nutrient solution will just about saturate a gram of sand, some comparisons can be made. It is very doubtful that the spodosols in the Amazon could release fresh cations to equal daily applications of nutrient solution. Once the cations are removed from the bonding sites, it may take considerable time to replace them with fresh cations because of the low concentrations of weatherable minerals.

Hewitt (1966) in discussing nurient solutions for sand culture of tomatoes and similar crops describes nutrient solutions with 120 ppm Ca, 48 ppm Mg, 31–62 ppm Na and 390 ppm K. Table 5 shows a range of extra table cation of 600–1,070μg/g (ppm) Ca, 48–180μg/g (ppm) Mg, 10–25μg/g Na, and 250–460 μg/g K in the Peru surface soils. In these soils, there was more than enough immediately available Ca, Mg, and K for crop growth. At 20–22 cm depth, the Peru soils had 50–425μg/g Ca, 23–43μ/g Mg, 13–22μg/g Na and 103–182μg/g K, or about enough Ca with slight to marked deficiencies in Mg and K.

If the Ducke A, B, and C soils are considered, the highest and lowest concentrations of cations at any level studied were: Ca, 2–108μg/g, Mg, 1–39μ g/g, Na, 4–30μ g/g, and K, 12–320μ g/g (Table 5). All of the levels of Ducke soils were mildly to strongly deficient in available cations. None of these soils, without added fertilizer, could, in theory support a vigorous tomato crop. Greenhouse tests with three varieties of tomatoes planted in these soils under ideal temperature and light for tomatoes showed 0.5 to 2 cm growth in one month compared to 25 cm growth with nutrient solution added. Survival in the Amazon soils was 46% compared to 100% in Amazon soil plus nutrient solution.

The Rio Negro-Branco soils have (extractable) 4–30μg/g Ca, 2–76μg/g Mg, 11–140μg/g Na, and 378–680μg/g K (Table 5). These soils are deficient in one case for Mg, and supplied in excess with K. At least one collecting site would not apparently support tomatoes (as far as soil chemistry is concerned), although the other four sites were reasonably well supplied with extractable cations.

The nearby "capoeira" soils (all levels, extractable) had 10–65μg/g Ca, 3–8μg/g Mg, 9–24μg/g Na, and 14–74μg/g K. The "Capoeira" is significanly deficient in all four extractable cations. It is doubtful that there soil could support tomatoes at all. The Mg, Ca and K levels are within the range of anticipated deficiency symptoms.

If extractable cations are considered (Table 5), it is doubtful that the

Ducke mineral soils could supply the annual growth requirements of the forest. This is a strong argument for uptake of nutrients directly from organic matter.

e. Total Soil Cations (Biological)

There were between 20 and 30 times more total biologically important cations (from complete digestion with $HCLO_4$–HF) in all levels of the Peru soils studied than in the Brazil soils (Table 4). This agrees with the studies by Sioli (1966) who describe the lower Andean soils as quite rich. The Ducke soils are heavily leached and appear to have weathered from poor parent material producing only 1,280 to 1,824μ g/g of cations per gram of soil compared to 22,922 to 30,465μ g/g from Peru soils. In many of the Brazil soils, the μ g/g of total cations was less than the C.E.C or potential bonding sites (Table 4). In light of the percent saturation data, this means that many of the cations in these sands were held on colloids and that little unweathered mineral remains in the upper soil horizons which can release cations usable by the plant. Or, if all of the biologically important cations measured in some Brazil soils were released at one time by accelerated weathering, they would not saturate all of the potential bonding sites. This is not true in Peru where many more total cations of biological importance occurred than available bonding sites. The low content of unweathered minerals capable of freeing usable cations and the low amounts of extractable cation suggests that the Amazon forests may be headed for a period of slow decline when the roots and leaching deplete all usable nutrients from the root zone.

The percent of the total cations which is not extractable and which is still potentially available through weathering is surprisingly contant, except for Rio Negro-Branco (Table 4). The 94.6% to 97.5% of cation reserves still available in Peruvian soils represents a much larger supply of nutrients (30,465–32,238μg/g) than the 94.8 to 98.6% reserved in Ducke soils (1,280–1,824μ g/g). There is a trend for increasing percentages of nonextractable cations with depth which agrees with the lower C.E.C and lower organic content with depth. The exceptions again are the Rio Negro-Branco area with soils which decreased in percent nonextractable cations with depth. Rio Negro-Branco had a high percent saturation and the least percents (79.0 and 63.4%) of nonextractable cations indicating that a fair proportion of the cations in this soil were bonded to colloids (largely organic) and free to move through the system. The adjacent "capoeira" had 94.9 and 89.1% nonextractable cations suggesting a low level of bonded cations available for uptake. This area was logged and burned four years ago and the present low cation content would be expected in view of the results of Nye & Greenland (1964) in Ghana. Care ful studies of month-to-month changes in the elemental content of the Amazonian forest ecosystem after burning are needed to complete the picture.

The diffuse deep root systems common in the "capoeira" appear to be well-suited to recovery of the dispersed, soluble nutrients released by burning. There are no data here to indicate whether deep roots exist in the climax forest or whether these are capable of bringing amounts of fresh nutrients into

TABLE 6. *Averages and ranges of total content of ten biologically important elements in μg/g for various depths (in cm) of Amazon soils on 5 to 10 samples each, (R = range, Av = average).*

Elements μg/g

Location	Depth-cm		Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N
Peru	0-4	R	1.5—37.5	1,725—18,500	525.0—9,025.0	55.0—1,150.0	1,200—5,670	650—20,000	200—4,600	115—1,425	861—5500
		Av	17.4	11,704	2,400.0	417.5	3,362	10,629	1,917	735	3185
	20-22	R	2.5—30.0	1,750—15,000	800.0—4,500.0	107.0—1,650.0	400—4,150	500—15,250	200—4,500	175—875	276—5,088
		Av	18.4	9,416	1,437.5	619.8	1,692	7,250	1,591	645	2,362
	60-62	R	10.0—28.5	1,725—13,250	650.0—1,050.0	69.0—200.0	2,950—6,500	2,550—20,000	200—1,550	925—1,475	246 3,480—
		Av	21.7	10,234	862.5	159.8	4,738	14,325	774	1,144	2,076
Brazil Ducke A	0-4	R	2.5—10.5	980—1,450	10.0—25.0	1.0—4.3	25—38	50—88	37—133	29—68	1,168—1,291
		Av	4.6	1,055	17.3	2.0	31	63	65	39	1,220
Ducke A	20-22	R	2.5—6.8	1,090—1,550	30.0—37.5	1.0—4.3	25—1_20	50—160	16—85	38—55	614—830
		Av	4.2	1,331	33.2	3.4	52	75	65	46	659
Ducke A	60-62	R	3.3—20.5	1,065—1,675	16.3—65.0	3.8—5.5	25—65	50—75	19—195	25—64	300—538
		Av	8.2	1,307	42.0	3.3	34	60	63	50	441
Ducke B	0-4	R	3.3—4.3	955—1,550	6.3—32.5	2.0—5.0	10—55	50—145	14—56	19—479	1,076—2,152
		Av	3.8	1,193	17.0	3.7	28	100	40	136	1,577
Ducke B	20-22	R	2.5—4.0	1,000—1,550	32.5—46.3	2.3—6.3	25—33	60—195	16—127	31—102	466—768
		Av	3.4	1,236	40.8	4.8	28	125	81	60	612
Ducke B	60-62	R	2.5—2.5	1,500—1,525	30.0—35.0	2.0—2.0	15—60	50—88	22—68	33—56	329—391
		Av	2.5	1,515	31.6	2.0	35	68	37	40	354

TABLE 6 (*contd.*)

Location	Depth-cm		Elements μg/g								
			Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N
Ducke C	0-4	R	2.0— 7.3	825— 1,475	30.0— 52.5	3.5— 20 5	75— 125	24— 370	15— 62	68— 328	4,366— 10,576
		Av	4.7	1,270	44.0	11.5	97	189	39	175	7,242
Ducke C	20-22	R	4.2— 4.6	1,070— 1,690	30.1— 67.6	10.1— 21.0	116— 140	64— 430	120— 124	88— 101	533— 560
		Av	4.3	1,347	37.9	15.8	128	218	122	93	546
Ducke C	60-62	R	2.5— 2.6	600— 650	30.5— 32.5	1.0— 1.0	25— 26	50— 55	42— 43	15— 17	480— 507
		Av	2.5	628	31.1	1.0	26	51	42	16	492
Brazil Borba	0-4	R	6.5— 7.3	1,475— 1,825	45.0— 72.5	12.5— 18.0	70— 123	230— 310	22— 92	233— 425	10,560— 10,981
		Av	7.1	1,690	57.1	14.6	84	272	55	354	10,753
Borba	20-22	R	4.5— 4.5	1,700— 1,726	80.5— 82.5	8.0— 10.0	85— 89	170— 180	112— 121	30— 34	1,245— 2,060
		Av	4.5	1,714	81.9	8.8	85	176	118	31	1,562
Bio Negro- Rranco	0-4	R	5.0— 12.8	1,300— 1,700	17.5— 52.5	5.0— 24.5	10— 108	240— 650	22— 31	91— 418	8,332— 9,223
		Av	8.7	1,590	38.0	15.0	72	417	26	324	8,704
Rio Negro- Branco	20-22	R	6.0— 6.8	1,015— 1,125	65.0— 71.3	10.0— 11.5	125— 140	675— 815	31— 56	43— 49	3,797— 4,565
		Av	6.1	1,100	67.4	10.8	133	737	42	44	4,095
"Capoeira"	0-4	R	3.3— 7.3	750— 1,675	22.5— 45.0	5.0— 7.5	13— 60	318— 608	14— 151	87— 206	479— 1,722
		Av	4.5	1,168	31.3	6.3	46	429	128	128	802
"Capoeira"	20-22	R	2.5— 3.3	1,015— 1,750	23.8— 52.5	4.8— 8.8	73— 95	390— 675	37— 126	25— 189	399— 907
		Av	2.9	1,416	37.0	7.3	86	469	92	88	615

the system. Observations of uprooted trees in the climax forest showed that few feeder roots occurred in the lower soil layers, and that most activity was limited to the upper layers in the wetter Brazil soils.

The analyses of total and ranges of elements (Table 6, 7) and those elements which are significantly higher (by paired sites) show a relatively wide range of elements in the soil. Some portions of each element occur as mineral reserves while other portions are in available form. In general, the soils of the Amazon Basin differed less in the amounts of the various elements present than did the plant materials from these same soils. For this reason, some levels from Ducke A and B, most of the Borba, Rio Negro-Branco, and "capoeira" soils are excluded from the significance listing (Table 7). For those soils not listed, fewer than three elements differed significantly in elemental content.

Those Brazilian soils which were most significantly different were the Ducke C soils. Ducke C 0–4 cm and Ducke C 20–22 cm were significantly higher (1% level) than the 60–62 cm level (Ducke C) in Cu, Fe, Mn, Na and Ca, suggesting that the 20–22 cm level is an accumulation zone. More samples at different depths are needed to accurately locate the zone of cation accumulation. Drainage and aeration relations are probably more important to the type of plants living here than is soil chemistry. Periodic flooding may account for nutrient differences in the wet site soils and plants.

The Ducke C surface soil was significantly higher (1% level) in total N than all other levels. Nearly all surface soil (0–4 cm) samples were consistently higher in N than the deeper levels, even for those locations not included in Table 1. The majority of roots in this "igapo" soil were located in the top 30 cm. The accumulation of heavy cations in the wet soil was expected. The 0–4 cm Ducke C soils were significantly higher in Mn, Zn, Na, K, and N than were the Ducke A and B 0–4 cm soils. Ducke C soils (20–22 cm) were significantly higher than the Ducke A 20–22 cm soils in Zn, Na, K, Ca, and Mg. Ducke B soils adjoin Ducke C to the east, but the B 0–4 cm level was significantly lower in Mn, Zn Na, K, and N than was the same zone for C. At 60–62 cm, Ducke A and B soils were higher in Fe, Zn, and Mg than were the 60–62 cm C soils. The 60–62 cm level is in the water table for the C soils, but not for the A and B soils which may account for leaching of the former, and the apparent accumulation in the 20–22 cm zone.

There were no significant differences among levels of the "capoeira" soils (except for Na) and all soil levels of Rio Negro-Branco and the "capoeira" were significantly higher than the Rio Negro-Branco roots, litter, and leaves in five and two elements respectively. There is a fairly high degree of variability in the "capoeira" soils, but these soils have fewer extractable cations (Table 4), and the same general levels of total elements as most other Brazil soils.

The most consistently significant differences in elemental content of all levels of soils occurred between the Peru and Brazil soils (Tables 6, 7). The Peru soils were significantly higher in all elements (1% level) than were the Brazil soils. The vegetation of Peru was also higher in all elements except

TABLE 7. *Comparison of soil areas by depth and location for significance of total elemental content at the* 1% *levels* (based on comparisons of 5 to 10 samples each, — significantly higher of the pair at the 5% level, —— significantly higher of the pair at the 1% *level; NB = Rio Negro-Branco*)

Location	Depth cm	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N
Ducke C	0-4									——
Ducke C	20-22					——		——		
Ducke C	0-4	——	——		——	——			——	——
Ducke C	60-62									
Ducke C	20-22	——	——		——	——		——		
Ducke C	60-62									
Borba	0-4	——			——		——		——	——
Borba	20-22			——				——		
NB	0-4		——						——	——
NB	20-22			——		——	——	——		
Ducke A	0-4									
Ducke C	0-4			——	——	——	——			——
Ducke B	0-4									
Ducke C	0-4			——	—	——	—			——
Ducke A	20-22									
Ducke C	20-22				——	——	—	——	——	
Ducke B	20-22									
Ducke C	20-22				——	——			——	
Ducke A	60-62		——		——				——	
Ducke C	60-62									
Ducke B	60-62		——		——		—		——	
Ducke C	60-62									——
NB	0-4		——						——	——
NB	20-22			——		——	——	——		
NB	0-4	——	——		—		——		——	——
Ducke Tot.	0-4									
Ducke Tot.	20-22									
NB	20-22	——		——		—	——	—		——
Borba	0-4	—	——	——	——		——		——	——
Ducke Tot.	0-4									
Borba	20-22		——	——						——
Ducke Tot.	20-22								—	
Peru	0-4	——	——	——	——	——	——	——	——	——
Brazil	0-4									
Peru	20-22	——	——	——	——	——	——	——	——	——
Brazil	20-22									
Peru	60-62	——	——	——	——	——	——	——	——	—
Brazil	60-62									

Na and a number of elements from roots. The high levels of total Na in the Peru soils and the relatively low levels of total Na in the Peru vegetation suggest that little Na is in available form in these soils, or that the plants take up small amounts of this cation which appears to have a minor role in growth. The data on extractable Na (Table 5) supports the former view since the levels of extractable Na in Peru were nearly the same as the levels of extractable Na in Brazil soils.

The few determinations of organic P showed a tendency for higher organic P in the 0–4 cm soils which also had higher organic contents (Table 2). Since standard tests for total P failed to show measurable levels of P in most mineral soil samples, I concluded that most of the P in the soil was in the organic phase and potentially available through direct or indirect nutrient cycling. The greatest accumulation of elements should occur in the dry season since there is less leaching rain, but inorganic P does not appear to accumulate in these surface soils (Sioli 1966). Organic P from 0–4 cm ranged from 1,600 to 21,400μg/g, with the Peru soils surprisingly low in organic P (Table 6). The 21,400 μg|g P occurred in the "capoeira" soil and agrees with the increase available P after burning found by Nye and Greenland (1960, 1964).

The total N level of Brazil soils is comparable to that reported by Moore and Adetunji (1966) for "normal" Ghana soils, but the total Mg and K levels are lower in Brazil. These observations agree with the Ghana (Cunningham 1962, 1963; Greenland and Kowal 1960; Greenland and Nye 1959) and the Nigerian studies (Vine 1946-47). The levels of Ca, Mg, K, and P (inorganic) agree with the findings reported by Sioli for Brazil.

If the total micronutrients in Peru soils are considered, there are adequate reserves of Cu, Fe, Mn, and Zn to supply the needs of rapidly growing plants, provided the cations which are available are in balance. Most of the Ducke and Borba soils have small but adequate reserves of total Cu, Fe, Mn, and Zn to support reasonable plant growth for a long time to come since these elements are needed in small amounts (Table 6). For example, if all of the reserve Cu were made available at one time, there would be about 250 times the level needed for good plant growth (Hewitt 1966) in a gram of soil , and much more in the total root zone. If all of the reserve Fe were made available at once, there would be a maximum of 2,500 times the daily level needed for plant growth (based on data for tomatoes). If all of the Mn were made available at one time, there would be a maximum of about 130 times the level needed. For Zn, there is only about 20 times the level needed for growth (Ducke, Table 6). These elements are needed at different levels, and the daily elemental demands of the climax and second growth rain forest vegetation is still unknown.

The data on micronutrients suggest that there is adequate Fe in the soil reserves for a very long time. The levels of Cu, Mn, and Zn are much lower. If the soil were supplying the major needs of the existing vegetation, without recycling and conservation, Cu, Mn, and Zn would probably be exhausted in a relatively short time, while continued podzolization would result in Fe and

Al accumulation at depth. There is a danger of imbalance of cations in these soils with further ageing, and a possibility of ultimate toxidity.

Looking at the sum of "available" and reserve nutrients in these soils, it is obvious that the lush rain forest must have an efficient means of obtaining nutrients stored in organic litter, since the soils are too depleted to support such growth. It is doubtful that the total μg of elements per gram of sandy soil studied in Brazil could support the present forest without direct nutrient cycling and other mechanisms such as nutrient withdrawal from senescent leaves and nutrient recharge from rain. Unfortunately, we do not know the rate at which the existing forest uses available nutrients, but the low nutrient content of soil water suggests that much of the nutrients released daily from organic decay travel back into vegetation directly, not through the soil solutions. It is doubtful that weathering of soil minerals could release nutrients fast enough to meet the needs of the existing vegetation. It is also doubtful that atmospheric recharge plus weathering of soil minerals would be sufficient to support rain forest nutrient requirements. Unfortunately, there was no opportunity to measure nutrient recharge from rain.

There is evidence from these data that the Amazonian rain forest could not for long maintain its present biomass on either the extractable or total nutrient reserves of the mineral soil alone. The Peruvian Amazon is an exception to this since the reserve of 30,465 μg/g of cations would be expected to support forest on its mineral reserves, augmented by atmospheric recharge, for many hundreds of centuries. The present climax forest in Brazil on soils depleted of weatherable minerals, even though it may be supported by mechanisms for nutrient conservation, should endure for a lesser time since, although the atmospheric additions will continue to enrich the system, and leakage from the "closed cycle" is aparently small (Klinge and Ohle 1962), the annual amount of nutrient release per gram in the root zone is predicted to decrease more noticeably than on richer soils. Since some of the soil deposits in the Amazon Basin were derived from the slopes of the Andes and Guiana highlands where rich soils occur today under heavy rainfall, it is probable that once the Amazon soils were richer than they are today. The Peruvian climax rain forest had a surface mycorrhizal root system and considerably more feeder roots (4–5 $\times$) at 60 cm than occurred in Brazil. This difference in root habit suggests that the trees were able to utilize nutrients released from the surface litter and deep soil. The Peruvian forest is superior in size and diversity to the Brazilian forest, probably because of richer soils.

Comparison of Plants and Soils

To compare plant and soil elemental levels, averages for all main elements from Brazil leaves, wood, bark, roots, litter, and litter fall, and averages for total elemental content (main elements needed by plants) and main extractable cation from all levels of Brazil soil were converted to μe (microequivalents). This makes it possible to examine the active levels of elements on a comparable basis (i.e. ability to take part in chemical reactions).

TABLE 8. *Comparisons of levels of elements in plant material and soils (in microequivalents per gram of dry matter from the Amazon, based on 45 samples). Elements μe/g*

Material	Elements μe/g										Total Elements
	Cu	Fe	Mn	Zn	Na	K	Ca	Mg	N	P	
Plants Averages of Total *Brazil*:											
Leaves	0.25	2.60	0.29	0.50	13.00	191.00	147.80	218.30	6,536.00	176.00	7,286
Wood	0.01	0.44	0.07	0.22	9.30	42.80	37.30	23.20	973.00	19.00	1,105
Bark	0.20	0.67	0.17	0.29	20.70	79.70	321.50	130.60	3,329.00	60.00	3,943
Roots	0.31	12.20	0.34	0.87	21.10	55.10	50.20	120.60	4,600.00	99.00	4,960
Litter	0.24	7.10	0.42	0.43	16.90	32.20	169.60	165.00	4,375.00	48.00	4,815
Litter Fall	0.24	5.53	0.27	0.39	45.70	58.20	180.30	166.80	3,845.00	78.00	4,380
Total	1.25	28.53	1.56	2.70	126.70	459.00	906.70	824.50	23,650.00	480.00	26,489 μe/6g or 26.5 me/6g
Soils *Brazil*											
Average of all levels	0.16	45.70	1.43	0.30	2.80	6.00	4.40	10.50	973.00*	——* ×6=	1,044 μe/g 6,264 μe/6g
Average Extractable	—	—	—	—	1.10	3.16	1.39	0.78	—— 6·45 μe/g	—— ×6 –	38.7 μe/6g

*Organic and inorganic soils, P was excluded since nearly all P was in the organic matter.

These data (Table 8) show that leaves had the greatest quantity of total elements relative to other plants parts, (1,286μe), roots were second in order (4,960μe), litter was next with 4,815μe, leaf fall was still lower at 4,430μe bark was next with 3,943μe, and wood was the lowest (1,105μ). Except for roots which had a slightly high ash weight resulting from mineral inclusions not removable by washing, this agrees with the percent ash data.

The roots were highest of all plant parts in Cu, Fe, and Zn (Table 8). Litter fall was high in Na, relative to other plant parts. Litter averaged higher in Mn, and leaves were higher in K, Mg, N, and P, while bark was high in Ca (relative to other plant parts).

Although it may not be fair to compare the amounts of total elements in the 6g of plant material (all types) to the average amounts of total elements needed by plants in 6g of soil (all levels), this was the only means available for determining where the bulk of elements occurs in the Amazonian ecosystem. When plant material becomes litter, all of the elements contained in the litter become potentially available, and within a relatively short time. The total biological elements in soils become available at a relatively slower rate. The total depth and mass of soil under an area 1 m^2 is probably greater than the total mass of vegetation occupying the top of the m^2 in deeply weathered soils. The only fair comparison of total relative elemental content would be between the available elements in the mass of soil actually tapped by plants, roots, and the elements in the mass of vegetation covering the 1 m^2. Such an approach was not practical in this study. It is practical but not totally accurate to compare the amounts of elements (on a gram for gram basis) essential to plants in a given mass of soil to the amounts of the same elements in the same mass of vegetation (dry weights), provided it is understood that there is a difference in the biomass of the vegetation versus the mass of soil actually supporting it.

Table 8 shows 26,489μe of total elements is 6g of plant material (av. of leaves, wood, bark, roots, litter and litter fall) to 6,264μe of total elements in 6g of soil, or 4.2 times total active elements in plant material. If ranges of elements in plants and soils are used, the same trend holds true. Thus, on a stoichiometric basis, the majority of elements are held in the organic phase of the Amazonian rain forest ecosystem, although we cannot correct for the total mass of soil versus plants for this study.

Low levels of foliar and soil Na could limit the numbers and abundance of larger salt-requiring (NaCl) mammals which are sparse in these forests partly because of hunting, and possibly from nutrient deficiencies. When the vegetation is destroyed by cutting and burning, the bulk of these elements are made soluble, and a large portion is lost through leaching and washing.

Since only small amounts of the total elemental reserves are actually "available" (1.5–21.0%, Table 4), the power of these podzolized soils to support vegetation is actually very low. There are a total of only 39μe/6g (soil) of extractable and theoretically available cations (Na, K, Ca, Mg only) in the Brazil soil (average of all levels) compared to average of 26,489μe in 6g

of plant material or 680 times more elements in plants which can be made available in about one day (5.4 g m^{-2} day^{-1} rate of litter decay). Vegetation is expected to concentrate nutrients from soil, but the low levels of extractable elements present today in Brazil soils leave little to concentrate. These findings support the view that the Amazoian rain forest on spodosols is on its way slowly to the decline phase when soil nutrients will gradually be exhausted. Burning results in only temporary enrichment of the soils with a subsequent rapid loss of nutrients. Future intelligent use of the rain forest requires a thorough understanding of the role of fire in the ecosystem, and the functioning of nutrient cycling. It is most likely that only crops or timber trees with mycorrhizal root systems can profitably be grown on the podzolized soils. The forests of the Amazon do not represent vast, untapped regions for agricultural exploitation, but rather an old, perhaps fragile system closely adapted to efficient nutrient utilization and conservation.

SUMMARY AND CONCLUSIONS

The direct nutrient cycling hypothesis states that on poor Amazonian sands nutrients are transported from dead organic litter by mycorrhizal fungi to living surface tree roots. In second growth forests, the trees have deep, diffuse roots which concentrate nutrients dispersed through burning and leaching. The gradual change in the old lake sediments has produced extremely poor soils which were covered initially by forests largely lacking in mycorrhizal root systems, and as the soil became poorer, these were replaced by predominantly mycorrhizal trees. In time, the soil of the root zone is expected to become depleted of nutrients usable by plants, and slow leakage from direct nutrient cycling will gradually reduce the nutrient reserves of the system resulting in an ultimate loss of rooted plants and renewed erosion begining the cycle over again. When the climax forest is cut and burned, nutrients stored for thousands of years in the organic phase of the ecosystem are suddenly made soluble and large amounts are lost to leaching and washing causing an accelerated decline of the nutrient level of the entire system.

The soils were podzolized sands with from 28.7% to 14.8% organic matter in the surface (0–4 cm) and less organic matter (6.1 to 3.7%) at 60 to 62 cm. Soil pH ranged from 6.1 to 3.7 at 0 to 4 cm, and 5.3 to 4.0 at 60 to 62 cm. The Peru soils proved to be richer than the Brazil sites and had the highest cation exchange capacity (C.E.C. 6,388μg/g, 0–4 cm), a moderate percent saturation (21.6%), with the highest total soil cations (30,465μg/g), and the highest sum of extractable cations (1,356μg/g) of all soils studied. The Rio Negro-Branco soils were the richest of the Brazil soils in most elements, but most soils studied in Brazil differed in minor degree from site to site. The "capoeira" or second growth soils were generally poor in all elements, and especially low in extractable Na, K, Ca, and Mg compared to the neighboring soils with climax forest. Many Brazil soils differed significantly by less than three elements. Ducke C soils (flooding land) were significantly higher than neighboring soils in Mn, Zn, Na, K, and N. Burning temporarily enriches the soil, but

leaching soon removes bases and leaves the total ecosystem much poorer in nutrients than before burning.

The Peru soils had sufficient elements to support plant growth by nutrient solution standards, but Brazil soils were deficient in all elements needed by plants. Soils rich naturally or temporarily enriched by burning have diffuse and surface roots, while the poorest soils have mainly surface mycorrhizal roots.

Six grams of plant material (dry weight compared gram for gram) averaged 26,489μe of total elements, while 6g of soil averaged (all levels studied) 6,264μe of total elements, and 39μe of extractable elements (Na, K, Ca, Mg). These data cannot be corrected here for the total mass of vegetation and soil involved in the ecosystem.

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